ADDITIONAL MORPHOLOGICAL MEASUREMENTS OF *ARCEUTHOBIUM SISKIYOUENSE* AND *A. MONTICOLA* (VISCACEAE)

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ABSTRACT

Additional morphological measurements were collected for *Arceuthobium siskiyouense* from a total of 15 locations in southwestern Oregon and northwestern California. Measurements were made for male and female plants growing on *Pinus attenuata, P. jeffreyi*, and *P. contorta* var. *contorta*. Characters measured were similar on all three hosts, but plant size was largest on *P. jeffreyi* and smallest on *P. contorta* var. *contorta*. Additional morphological measurements were also collected for *A. monticola*, another endemic dwarf mistletoe of the Klamath/Siskiyou Mountains. Results demonstrated that *A. siskiyouense* is morphologically similar to *A. campylopodum* and that *A. monticola* is morphologically similar to *A. californicum*. Our measurements for flower characteristics are the first reported for *A. siskiyouense* and *A. monticola*.

Key Words: *Arceuthobium monticola, Arceuthobium siskiyouense,* morphology, *Pinus attenuata, Pinus contorta* var. *contorta, Pinus jeffreyi, Pinus monticola*

RESUMEN

Se reportan nuevas mediciones morfológicas de *Arceuthobium siskiyouense* de un total de 15 sitios en el suroeste de Oregón y noroeste de California. Las mediciones se hicieron sobre plantas masculinas y femeninas creciendo sobre *Pinus attenuata, P. jeffreyi*, y *P. contorta* var. *contorta*. Los caracteres medidos fueron similares en las plantas sobre todos los hospederos, pero el tamaño de la planta fue mayor sobre *P. jeffreyi* y más pequeño sobre *P. contorta* var. *contorta*. También se reportan mediciones adicionales sobre *A. monticola*, otro muérdago enano endémico de las Montañas Klamath/Siskiyou. Los resultados muestran que *A. siskiyouense* es morfológicamente similar a *A. campylopodum* y que *A. monticola* es morfológicamente similar a *A. californicum*. Nuestras mediciones de las características de las flores son las primeras que se reportan tanto para *A. siskiyouense* como para *A. monticola*.

Palabras Clave: *Arceuthobium monticola, Arceuthobium siskiyouense,* morfología, *Pinus attenuata, Pinus contorta* var. *contorta, Pinus jeffreyi, Pinus monticola*

Arceuthobium siskiyouense Hawksw., Wiens & Nickrent (Knobcone pine dwarf mistletoe, Viscaceae) and *A. monticola* Hawksw., Wiens & Nickrent (western white pine dwarf mistletoe) are endemic to the Klamath/Siskiyou Mountains of northwestern California and southwestern Oregon (Hickman 1993; Hawksworth & Wiens 1996). Prior to 1992, *A. siskiyouense* was classified as *A. campylopodum* Engelm. and *A. montiolca* was grouped with *A. californicum* Hawksw. & Wiens. Hawksworth et al. (1992) separated *A. siskiyouense* from *A. campylopodum* based on differences in plant and fruit size, flowering period, host affinities, and the inducement of witches' brooms or not on infected principal hosts (see their Table 1). They separated *A. monticola* from *A. californicum* based on plant and fruit size, plant color, seed dispersal period, and host affinities (see their Table 2). An electrophoretic analysis of isozymes also supported the separation of *A. siskiyouense* from *A. campylopodum* and *A. monticola* from *A. californicum* (Nickrent & Butler 1991). However, recent molecular work has demonstrated that these taxa are closely related and that further study of their morphological and physiological characteristics was needed (Nickrent et al. 2004). Because *A. siskiyouense* commonly parastizes *Pinus attenuata* Lemm., *P. jeffreyi* Grev. & Balf., and *P. contorta* Dougl. ex Loud. var. *contorta* within its geographic range (Mathiasen & Daugherty 2009), we collected additional morphological data for this dwarf mistletoe from each of these hosts. We also collected additional morphological data for *A. monticola* because little was known regarding its flower and fruit morphology (Hawksworth & Wiens 1996). This allowed us to compare morphological characteristics of *A. siskiyouense* and *A. monticola* with *A. campylopodum* and *A. californicum*, respectively, using plant and flower characteristics for all four species.

MATERIALS AND METHODS

In order to make a comparison of the morphological characters of *Arceuthobium siskiyouense* on its pine hosts we sampled 15 populations of the mistletoe (Fig. 1). Plants were collected from *Pinus attenuata* only (3 locations); from *P. jeffreyi* only (2 locations); from both *P. attenuata* and *P. jeffreyi* (6 locations); and from both *P. attenuata* and *P. contorta* var. *contorta* (4 locations). Five populations of *Arceuthobium monticola* were sampled; 2 in southwestern Oregon and 3 in northwestern California (Fig. 1). Plants were measured from the type localities for both dwarf mistletoes (Fig. 1; locations 5 and 6; Hawksworth et al. 1992). Identification of host trees was based on Hickman (1993) and Critchfield (1980) for *P. contorta* var. *contorta*.

From each population, 10–20 male and 10–20 female infections were collected and the dominant shoot from each infection was used for morphological measurements. The dwarf mistletoe plant characters measured were those used by Hawksworth and Wiens (1996) for taxonomic classification of *Arceuthobium* spp. The following morphological characters were measured: 1) height, basal diameter, third internode length and width, and color of male and female plants; 2) mature fruit length, width, and color; 3) seed length, width and color; 4) length and width of staminate spikes; 5) staminate flower diameters for 3- and 4-merous flowers; 6) length and width of staminate flower perianth lobes; and 7) anther diameter and anther distance from the perianth lobe tip. Plants were measured within 24 hours after collection and were measured using a digital caliper, a dissecting microscope with a micrometer, or with a 7× hand lens equipped with a micrometer. Staminate spike and flower measurements were made during the peak of anthesis and fruit and seed measurements were made during the peak of seed dispersal.

Because the times of flowering and seed dispersal for both dwarf mistletoes were poorly known (Hawksworth & Wiens 1996), additional observations of the phenology of these taxa were made during the summer and fall of 1998, 2003, 2004, 2007, and 2008.

RESULTS AND DISCUSSION

Arceuthobium siskiyouense

Plant heights for male and female plants on the pine hosts of *Arceuthobium siskiyouense* were similar, but plants were slightly smaller from *Pinus contorta* and slightly larger from *P. jeffreyi* when compared to those measured on *P. attenuata* (Table 1). The means and ranges for basal diameters and third internode dimensions were also similar for male and female plants from the different pine hosts. Flower characteristics were also similar, but the diameter of 3-merous flowers was smaller by 0.2–0.3 mm from male plants growing on *P. contorta* (Table 1). Fruit and seed sizes followed the same pattern as plant heights; fruits and seeds were largest on average from *P. jeffreyi* and smallest from *P. contorta*. Plant color of both male and female plants ranged from dark brown to red-brown to brown-green, independent of the host from which they were sampled. The dark brown to red-brown color of plants was the principal characteristic used to identify *A. siskiyouense* at two locations where there were no infected *P. attenuata* growing near infected *P. jeffreyi* (Fig. 1, locations 7 and 19).

The mean size of plants reported by Hawksworth et al. (1992) when they described *A. siskiyouense* was similar to what we obtained, but we measured plants on *P. attenuata* that were larger (15 cm) than they reported (10 cm). We also found that the basal diameters and third internode dimensions of *A. siskiyouense* plants were slightly larger than those reported by Hawksworth el al. (1992). Results also indicate that the size of fruits of *A. siskiyouense* was larger (5.1 × 3.3 mm) than reported by Hawksworth et al. (1992) for this species (4.0 × 2.5 mm) or by Hawksworth and Wiens (1996) (3.6 × 2.1 mm).

The results of our morphological measurements for *Arceuthobium siskiyouense* demonstrate that this species is morphologically very similar to *A. campylopodum* (Table 2). The latter taxon originally encompassed *A. siskiyouense* before Hawksworth et al. (1992) separated the dwarf mistletoe populations parasitizing *Pinus attenuata* in northwestern California and southwestern Oregon at the specific level. Based on our measurements of *A. siksiyouense*, the size of plants, flowers, and fruits are only slightly larger than those of *A. campylopodum*; the primary morphological difference between these species being plant color. *Arceuthobium siskiyouense* is

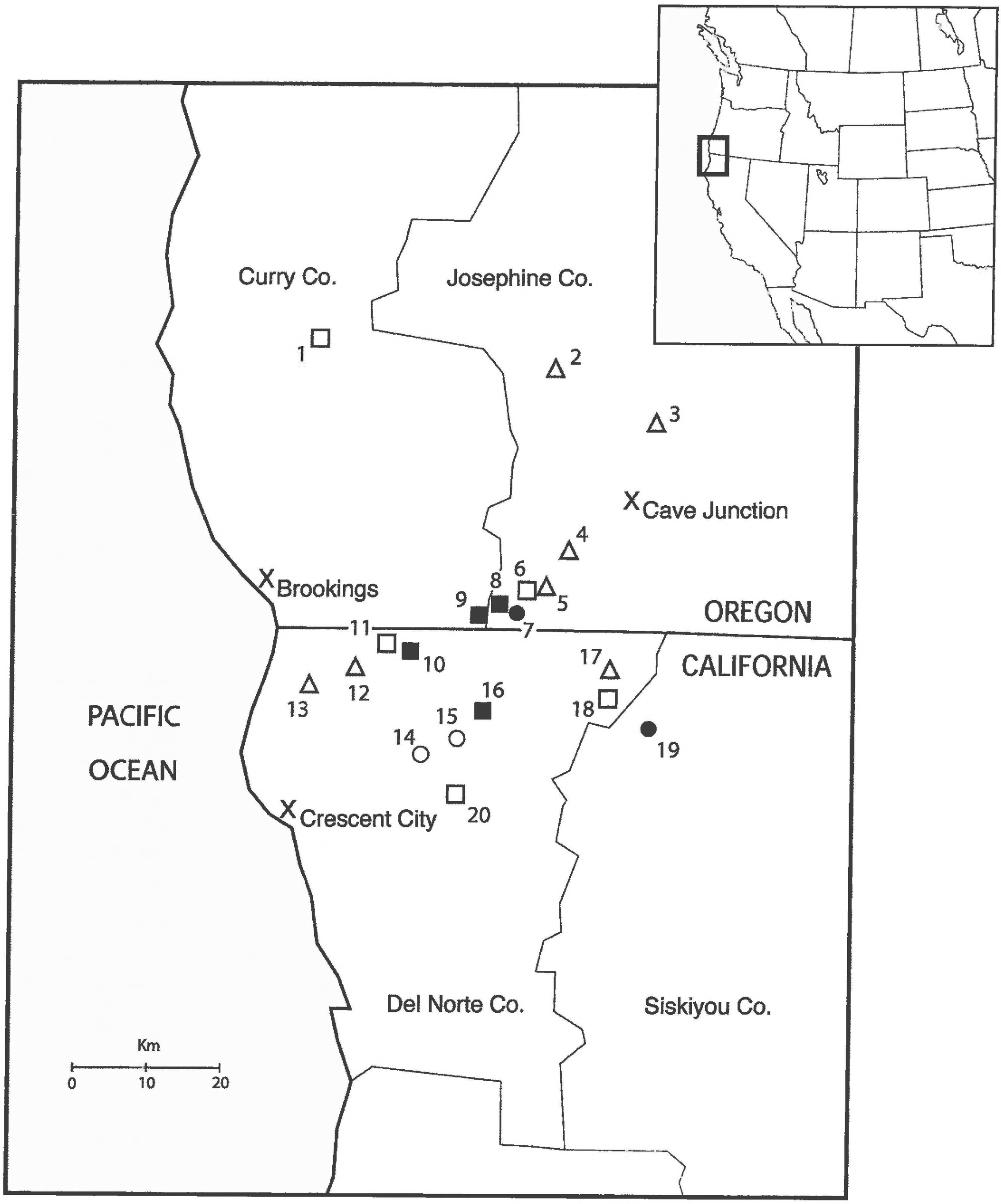

FIG. 1. Approximate location of collection sites in California and Oregon. **Open triangles** represent locations where *Arceuthobium siskiyouense* was collected and measured on *Pinus attenata* and *P. jeffreyi*. **Open circles** represent locations where *A. siskiyouense* was collected and measured on *P. attenuata* only. **Dark squares** represent locations where *A. siskiyouense* was collected and measured on *P. attenuata* and *P. contorta* var. *contorta*. **Dark circles** represent locations were *A. siskiyouense* was collected and measured only on *P. jeffreyi*. **Open square** represent locations where *A. monticola* was collected and measured on *P. monticola*. Numbers correspond to the following locations: 1–Snowcamp Mountain; 2–Chrome Ridge; 3–Lookout Gap; 4–Rock Creek on Oregon Mountain Road; 5–Type locality for *A. siskiyouense* on Oregon Mountain Road; 6–Type locality for *A. monticola* on Oregon Mountain Road; 7–Oregon Mountain; 8–Bain Station; 9–3 km southwest of Bain Station; 10–Smith River Bridge; 11–Sourdough Junction; 12–Pine Flat Mountain; 13–High Divide; 14–Old Gasquet Toll Road, near Danger Point; 15–Old Gasquet Toll Road, Elevenmile Creek; 16–Old Gasquet Toll Road, Twelvemile Creek; 17–5 km north of Black Butte; 18–Black Butte; 19–Bear Gulch; 20–Ship Mountain.

TABLE 1. Morphological measurements for *Arceuthobium siskiyouense* on *Pinus attenuata*, *P. jeffreyi*, and *P. contorta* var. *contorta*. Data are listed as mean (range) [n]. Letters in brackets designate sample sizes already listed in the same column. Plant heights in cm and all other measurements in mm.

Character	*Pinus attenuata*	*Pinus jeffreyi*	*Pinus contorta* var. *contorta*
Plant Height			
Male	8.1 (5.1–15.2) [120a]	8.3 (5.1–14.7) [100a]	7.7 (5.0–13.9) [60a]
Female	8.9 (5.3–14.8) [160b]	9.3 (5.8–17.3) [120b]	8.7 (5.7–14.1)[a]
Basal Diameter			
Male	3.0 (1.8–4.3) [a]	3.1 (2.4–6.1) [a]	2.9 (2.1–5.1) [a]
Female	2.9 (1.9–5.7) [b]	3.2 (2.4–5.9) [b]	3.0 (1.9–4.9) [a]
Length of Third Internode			
Male	11.7 (7.1–22.3) [a]	12.8 (7.5–22.9) [a]	11.3 (6.3–21.2) [a]
Female	12.5 (7.4–22.8) [b]	14.7 (7.5–25.4) [b]	12.7 (5.8–20.7) [a]
Width of Third Internode			
Male	2.0 (1.5–2.8) [a]	2.2 (1.6–3.0) [a]	1.9 (1.2–2.8) [a]
Female	1.9 (1.3–3.0) [b]	2.1 (1.6–3.0) [b]	1.9 (1.4–2.8) [a]
Staminate Spike Length	11.1 (6.0–17.3) [200c]	12.4 (5.2–19.1) [160c]	10.5 (6.2–15.8) [100b]
Staminate Spike Width	1.9 (1.5–2.4) [c]	2.0 (1.6–2.6) [c]	1.9 (1.4–2.3) [b]
Mean Flower Diameter			
3–merous	3.2 (2.6–3.9) [100d]	3.3 (2.7–3.8) [50d]	3.0 (2.5–3.7) [50c]
4–merous	4.4 (3.7–5.6) [d]	4.5 (3.7–5.9) [d]	4.4 (3.6–5.5) [c]
Perianth Lobe Length	1.5 (1.2–1.9) [c]	1.5 (1.1–2.0) [a]	1.5 (1.1–1.8) [b]
Perianth Lobe Width	1.5 (1.2–2.1) [c]	1.4 (1.1–1.9) [a]	1.4 (1.0–2.0) [b]
Anther Diameter	0.8 (0.5–1.1) [c]	0.7 (0.4–1.1) [a]	0.8 (0.5–1.2) [b]
Anther Distance from Tip	0.8 (0.5–1.1) [c]	0.8 (0.4–1.1) [a]	0.7 (0.4–1.0) [b]
Mean Fruit Length (mm)	5.1 (4.1–6.1) [110e]	5.3 (4.0–6.0) [80e]	4.9 (3.8–5.7) [c]
Mean Fruit Width (mm)	3.3 (2.6–4.1) [e]	3.5 (2.8–4.3) [e]	3.1 (2.5–3.8) [c]
Seed Length	3.0 (2.1–4.0) [e]	3.1 (2.0–3.9) [e]	2.9 (2.1–2.8) [c]
Seed Width	1.3 (1.0–1.8) [e]	1.3 (0.9–1.9) [e]	1.2 (0.8–1.8) [c]

consistently dark brown, red-brown, or brown-green, and we did not observe any male or female plants of this mistletoe that we considered yellow, a plant characteristic described for *A. campylopodum*. However, we did observe a few male plants of *A. siskiyouense* that were brown-green and it is difficult to determine if our use of brown-green to designate plant color is different from the olive-green designation used by Hawksworth and Wiens (1972, 1996) for *A. campylopodum*. It was also difficult to compare plant dimensions between these species because Hawksworth et al. (1992, Table 1) and Hawksworth and Wiens (1996, Table 16.6) indicate the height of plants of *A. campylopodum* as averaging 12 cm with a range from 10–14 cm. However, they describe *A. campylopodum* plants as averaging about 8 cm in height with a maximum height of 13 cm in their written descriptions of the species (Hawksworth & Wiens 1972, 1996). We chose to adopt their written descriptions of *A. campylopodum* for our comparisons with *A. siskiyouense* in Table 2.

The mean diameter of 3-merous flowers for *A. siskiyouense* and *A. campylopodum* was similar also (3.2 and 3.0 mm, respectively), but Hawksworth et al. (1992) and Hawksworth and Wiens (1996) did not provide a range for flower diameters of either species. Our flower measurements indicate the width of perianth lobes and anther diameters were smaller for *A. campylopodum* when compared to *A. siskiyouense* (Table 2), but other flower characteristics were similar for these taxa.

The mean dimensions of fruits of *A. siskiyouense* we obtained (5.1 × 3.3 mm) were approximately the same size as the fruits of *A. campylopodum* when information for this character reported in the descriptions of *A. campylopodum* in Hawksworth and Wiens (1972, 1996) is used (5.0 × 3.0 mm). But fruit dimensions

TABLE 2. Comparison of morphological characters between *Arceuthobium siskiyouense* and *A. campylopodum*. Morphological measurements for *A. siskiyouense* are combined from all hosts. Data for *A. campylopodum* are from Hawksworth and Wiens (1996, page 199). Single numbers in columns are means as no range information was available for *A. campylopdum*. Plant heights in cm and all other measurements in mm.

Character	*Arceuthobium siskiyouense*	*Arceuthobium campylopodum*
Plant Height[a]	8.7 (5–17)	8.0 (Maximum - 13)
Basal Diameter[a]	3.0 (1.8–6.1)	3.0 (1.5–5.0)
Length of Third Internode [a]	12.9 (6–25)	11.3 (7–22)
Width of Third Internode [a]	2.0 (1.2–3.0)	2.0 (1.5–2.5)
Plant Color	Dark brown, brown-green, red-brown	Olive-green, yellow
Mean Flower Diameter [b]	3.2	3.0
Perianth Lobe Length	1.5	1.4
Perianth Lobe Width	1.5	1.1
Anther Diameter	0.8	0.5
Anther Distance from Tip	0.8	0.8
Mean Fruit Length	5.1	5.0
Mean Fruit Width	3.3	3.0

[a] – Male and female plants combined.
[b] – 3-merous flowers.

of *A. campylopodum* have also been reported as large as 6.0 × 3.5 mm in Hawksworth et al. (1992, Table 1) and 5.6 × 3.0 mm in Hawksworth and Wiens (1996, Table 16.6). Therefore, it was difficult to compare not only plant dimensions for these dwarf mistletoes, but fruit dimensions as well. Nevertheless, when our measurements of characters for *A. siskiyouense* are compared with the written descriptions, it is evident these dwarf mistletoes are morphologically more similar than reported by Hawksworth et al. (1992). A more detailed morphological analysis is needed for *A. campylopodum*, as well as for other closely related California taxa such as *A. occidentale* Engelm. and *A. littorum* Hawksw., Wiens & Nickrent. The latter species are also morphologically similar to *A. campylopodum* as are their hosts, phenology, and molecular characteristics (Nickrent & Butler 1990; Hawksworth et al. 1992; Hawksworth & Wiens 1996; Nickrent et al. 2004).

Although Hawksworth et al. (1992) reported that *A. siskiyouense* did not induce the formation of witches' brooms on infected *Pinus attenuata*, our observations indicate that it frequently does form brooms on this host (Mathiasen and Daugherty 2009). Host susceptibility was also used by Hawksworth et al. (1992) to separate *A. siskiyouense* from *A. campylopodum*; *A. siskiyouense* rarely infecting both *P. jeffreyi* and *P. ponderosa* Laws., both of which are principal hosts of *A. campylopodum*. However, *A. campylopodum* commonly infects *P. attenuata*, the principal host of *A. siskiyouense*, and the latter species has now been shown to commonly parasitize *P. jeffreyi* (Mathiasen & Daugherty 2009).

Anthesis of *Arceuthobium siskiyouense* begins in late-July, peaks in mid-August, and continues into early-September. In every year we observed flowering for this mistletoe, it had completed flowering by late-September. Seed dispersal of *A. siskiyouense* begins in late-September and peaks in mid- to late-October. It continues into early-November, but we were not able to determine when seed dispersal is completed for this species. Our observations of seed dispersal for *Arceuthobium siskiyouense* agree with those reported by Hawksworth et al. (1992), but our observations of flowering indicate its peak flowering period is in August rather than in September.

Based on the morphological data presented here, the overlap in physiological characteristics of *Arceuthobium siskiyouense* with *A. campylopodum* (phenology and host affinities), and the molecular data available thus far (Nickrent et al. 2004), the classification of the dwarf mistletoe populations parasitizing *P. attenuata* in the Klamath/Siskiyou Mountains as a subspecies of *A. campylopodum* may be more representative

of the phylogenetic relationships of these mistletoes. Our data indicate that there are a few morphological discontinuities between *A. siskiyouense* and *A. campylopodum* and Nickrent and Butler (1991) found genetic differences between these taxa based on their isozyme analysis. However, until we collect additional morphological, host infection, phenology, and distribution data for *A. campylopodum* throughout its geographic range, we feel it would be inappropriate to recombine *A. siskiyouense* as a subspecies of *A. campylopodum* here. Furthermore, subspecies of *Arceuthobium* are usually geographically isolated (Hawksworth and Wiens 1996) and thus far we are uncertain to what degree the geographic range of these two mistletoes does or does not overlap, even though the distribution maps in Hawksworth and Wiens (1996) clearly indicate these species are sympatric. Although Nickrent et al. (2004) considered *A. campylopodum* and *A. siskiyouense* to be conspecific, this conclusion is based solely on molecular data and does not consider the morphological differences (plant color), phenology differences, or host susceptibility discontinuities between these populations. Further research is needed to clarify the host susceptibility of *P. ponderosa* to *A. siskiyouense* and *P. attenuata* to *A. campylopodum* discussed by Hawksworth et al. (1992) and Hawksworth and Wiens (1996). In addition, a detailed morphometric analysis of *A. campylopodum* is needed and this work should include analysis of the other mistletoes closely aligned with *A. campylopodum* in California: *A. occidentale* and *A. littorum*.

Arceuthobium monticola

Our morphological measurements of *Arceuthobium monticola* are summarized in Table 3. The plant dimensions we obtained for *A. monticola* were similar to those reported by Hawksworth et al. (1992), except that we measured plants that were larger (13 cm) than what they reported (10 cm). We also measured larger third internode and fruit dimensions than what they reported. The color of male and female plants of *A. monticola* was consistently dark brown, red-brown, or brown-green. Rarely male plants were brown-yellow to almost completely yellow, as are those of *A. californicum*. Our data include the first measurements of flower characteristics. Previous descriptions (Hawksworth et al. 1992) indicated that *A. monticola* only forms 3-merous flowers. However, we found that 3-merous flowers were usually more numerous on the same plant, but this character varied. The species produces both 3- and 4-merous flowers, and rarely 5-merous flowers, and we observed a few male plants that produced predominantly 4-merous flowers.

A comparison of morphological characters using our data for *Arceuthobium monticola* and those reported in Hawksworth and Wiens (1972, 1996) for *A. californicum* is presented in Table 4. Plant dimensions were approximately the same for both species, but plant color for *A. monticola* was usually dark brown or brown-green. However, some male plants were brown-yellow to yellow, as are those of *A. californicum*. Flowers and fruits of *A. monticola* were slightly larger on average than those of *A. californicum*, but seeds were smaller in length.

Although Hawksworth et al. (1992) and Hawksworth and Wiens (1996) reported that *Arceuthobium californicum* rarely parasitizes *Pinus monticola*, this is evidently based on one report of this mistletoe/host combination from Castle Lake Campground, west of Shasta City, CA (see Hawksworth and Wiens 1996, p. 334). Our field observations at Castle Lake, and our comparison of specimens of *A. californicum* and *A. cyanocarpum* (A. Nelson ex Rydb.) Coulter & Nelson, indicate the mistletoe infecting *P. monticola* at Castle Lake is *A. cyanocarpum*. Therefore, we consider there to be no confirmed reports of *A. californicum* on *P. monticola* at this time. We have observed *A. monticola* infecting *P. lambertiana* Dougl. at two locations in northern California, but this pine is clearly a rare host of *A. monticola* at both locations. In contrast, *P. lambertiana* is the principal host of *A. californicum*.

Anthesis of *A. monticola* begins in mid-July, peaks in early- to mid-August, and continues into early-September. Seed dispersal of *A. monticola* starts in early September, peaks in late September, and is finished by late October. While our observations of flowering for *A. monticola* agree with those reported by Hawksworth et al. (1992), our observations of seed dispersal indicate that peak seed dispersal for this species is in September, and not October to November. We consistently observed that *A. monticola* had completed seed dispersal by late October and did not extend this aspect of its life cycle into November as reported by Hawksworth et al. (1992).

TABLE 3. Morphological measurements for *Arceuthobium monticola* on *Pinus monticola*. Data are listed as mean (range) [n]. Letters in brackets indicate sample sizes already listed in the same column. Plant heights in cm and all other measurements in mm.

Character	A. monticola
Plant Height	
Male	7.8 (4.4–12.6) [50a]
Female	8.5 (6.1–13.4) [a]
Basal Diameter	
Male	2.8 (2.0–3.5) [a]
Female	2.9 (2.1–3.8) [a]
Length of Third Internode	
Male	9.9 (4.8–17.1) [a]
Female	11.5 (6.9–23.4) [a]
Width of Third Internode	
Male	1.7 (1.3–2.4) [a]
Female	1.7 (1.3–2.5) [a]
Staminate Spike Length	8.6 (5.0–14.2)[100b]
Staminate Spike Width	1.4 (1.1–1.8) [b]
Mean Flower Diameter	
3-merous	2.5 (2.0–3.1) [a]
4-merous	3.6 (3.0–4.6) [a]
Perianth Lobe Length	1.3 (0.8–1.7) [b]
Perianth Lobe Width	1.1 (0.7–1.3) [b]
Anther Diameter	0.5 (0.4–0.8) [b]
Anther Distance from Tip	0.6 (0.4–0.9) [b]
Mean Fruit Length	4.7 (4.0–5.6) [a]
Mean Fruit Width	3.0 (2.4–3.5) [a]
Seed Length	2.5 (1.8–3.2) [a]
Seed Width	1.2 (0.9–1.4) [a]

Our morphological data for *Arceuthobium monticola* further demonstrates its similarity to *A. californicum*, but these two species do have some morphological differences that can be used to distinguish them. While male and female plant sizes are similar and their ranges are nearly identical, the mean flower diameter of 3-merous flowers of *A. monticola* is smaller than that of *A. californicum*. In addition, the fruits of *A. monticola* are much larger and they are distinctly glaucous which causes them to appear blue, in contrast to the lightly-glaucous, green fruits of *A. californicum*. Plant color also distinguishes *A. monticola* (dark brown to brown-green) from *A. californicum* (yellow to green). Furthermore, *A. monticola* rarely parasitizes *Pinus lambertiana*, the principal host of *A. californicum* and thus far, *A. californicum* has not been confirmed to parasitize *P. monticola*, although this pine is common in the geographic range of *A. californicum* in the Sierra Nevada Mountains (Griffin & Critchfield 1972; Hawksworth and Wiens 1996). Although we have now collected *A. californicum* from the Klamath Mountains (near Etna and Orleans), its distribution still remains south of that for *A. monticola*, so thus far it does not appear that the geographic ranges of *A. monticola* and *A. californicum* overlap. Therefore, the classification of *Arceuthobium monticola* as a subspecies of *A. californicum* could be given consideration given the morphological, physiological, and molecular differences between them and their apparent geographic isolation (Nickrent & Butler 1991; Hawksworth et al. 1992; Nickrent et al. 2004). However, until we complete a detailed morphometric analysis with data for *A. californicum* from throughout its geographic distribution, we do not feel it would be appropriate to recombine *A. monticola* as a subspecies of *A. californicum* here.

Although the dimensions and color of male and female plants of *A. siskiyouense* and *A. monticola* were

TABLE 4. A comparison of morphological characters for *Arceuthobium monticola* and *A. californicum*. Data is listed as mean (range). Data for *A. californicum* is from Hawksworth et al. 1992 (Table 2) and Hawksworth and Wiens (1996, page 197). Single numbers in columns are means as no range information was available for *A. californicum*. Plant heights in cm and all other measurements in mm.

Character	A. monticola	A. californicum
Plant Height [a]	8.2 (4.4–13.4)	8.0 (6.0–14.0)
Basal Diameter [a]	2.8 (2.0–3.8)	2.0 (1.5–4.0)
Length of Third Internode [a]	10.7 (4.8–23.4)	10.5 (5.0–16.0)
Width of Third Internode [a]	1.7 (1.3–2.5)	1.5 (1.0–2.0)
Plant Color [a]	Dark brown, red-brown, brown-green or rarely yellow-brown or yellow	Yellow to greenish
Mean Flower Diameter [b]	2.5	3.3
Perianth Lobe Length	1.3	1.5
Perianth Lobe Width	1.1	1.1
Anther Diameter	0.5	0.5
Anther Distance from Tip	0.6	0.7
Mean Fruit Length	4.7	4.0
Mean Fruit Width	3.0	2.5
Fruit Color	Blue (highly glaucous)	Green (slightly glaucous)
Seed Length	2.5	3.2
Seed Width	1.2	1.2

[a] – Male and female plants combined.
[b] – 3-merous flowers.

also similar based on our findings, they differed in their flower characteristics for both 3- and 4-merous flowers, and fruit and seed sizes (compare Tables 1 and 3). In addition, *Pinus attenuata* is considered to be immune to infection by *A. monticola* (Hawksworth and Wiens 1996), a conclusion our field observations in several severely *A. monticola*-infested mixed stands of *Pinus monticola* and *P. attenuata* supports. Our field observations and those of Hawksworth and Wiens (1996) also indicate that *P. monticola* is immune to infection by *A. siskiyouense*. Furthermore, Nickrent and Butler (1991) found that these species were genetically different based on their electrophoretic analysis of isozymes.

A comparison of the descriptions of *Arceuthobium campylopodum* in Hawksworth and Wiens (1972, 1996) with our morphological and physiological data for *A. sikiyouense* and *A. monticola* could be interpreted as support for the classification of these species as conspecific with *A. campylpodum* as suggested by Nickrent et al. (2004), but could also support their recombination as subspecies of *A. campylopodum*. Whether or not these *Arceuthobium* taxa deserve taxonomic recognition as distinct species, subspecies, or are conspecific with *A. campylopodum* will continue to be debated by plant systematists, as well as forest managers and wildlife biologists whose interests in *Arceuthobium* spp. have economic and ecological implications (Hawksworth & Wiens 1996; Nickrent et al. 2004; Mathiasen et al. 2008). Clearly, further research is warranted on the morphological, physiological, and molecular relationships of the species discussed here as well as all the taxa included in Section *Campylopoda* by Hawksworth and Wiens (1996).

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